The Biology of the Northeastern Pacific Turridae. IV. Shell Morphology and Sexual Dimorphism in *Aforia circinata* (Dall, 1873)

by

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Abstract. The shell morphology of the boreal deep-water species Aforia circinata is examined, and a pronounced dimorphism in sexually mature animals is described. Mature females have a canal-like notch, which is lacking in males, midway down the outer lip. The notch is similar to, but smaller than the siphonal canal, and arises abruptly from a low ridge at an approximate shell length of 76 mm. The notch may function as an auxiliary siphonal canal during oviposition. No other sexual differences in shell shape of immature animals could be demonstrated, although small males are more variable in some measurements than are small females, or large animals of either sex. Healed shell fractures are common, and are probably due to attempted predation by crabs.

INTRODUCTION

WITH THE EXCEPTION of the cephalopods, sexual dimorphism has not been commonly demonstrated in mollusks. In prosobranch gastropods, sexually determined size dimorphisms have been reported in several lineages: for Cypraecassis (CLENCH & ABBOTT, 1943); Fasciolaria (WELLS, 1970); Mitra (CHESS & ROSENTHAL, 1971); Thala (MAES & RAEIHLE, 1975); Neptunea (MACINTOSH & PAUL, 1977); Buccinum (TEN HALLERS-TJABBES, 1979); and Drillia, Strictispira, Pilsbryspira (MAES, 1983). That females are larger than males within the stenoglossa may be a general trend that goes unnoticed due to the relatively large sample sizes needed to determine a statistically significant difference in the mean adult size between the sexes of any given population. Although MAES (1983) demonstrated size differences in four species of Caribbean turrids, no size differences have been observed in any northeastern Pacific turrids examined to date (SHIMEK, 1983a, b, c), even though sufficiently large samples have been examined in detail.

Sexually correlated differences in shape are even less common. The sexes of *Voluta musica* Linné, 1758, and *Voluta ebraea* Linné, 1758, are sufficiently different to be easily distinguished (CLENCH & TURNER, 1964), but whereas there are slight sexual differences in the shell shapes of *Buccinum undatum*, sophisticated mathematical and measuring techniques are needed to demonstrate them (TEN HALLERS-TJABES, 1979). *Neptunea* species also have a size dimorphism similar to that shown in *Buccinum undatum* (MACINTOSH & PAUL, 1977) and similar subtle shape differences may occur. Sexual shell-shape differences have not been reported in the toxoglossa, although "odd" shapes at variance to the typical shell shape have been noted for several tropical turrids (POWELL, 1964, 1969).

The northeastern Pacific boreal turrid Aforia circinata (Dall, 1873) is seldom collected, and ecologically poorly known; data on diet, habitat, reproduction, and population biology are lacking. During examination of specimens of this species, several individuals were found exhibiting the "odd" shape (Figure 1) described and figured by POWELL, 1969. I attempted to correlate this shape with other observable features of the organisms.

A characteristic of the immense prosobranch family Turridae is the presence of a secondary or anal notch. The position of this notch varies with the subfamily of turrids examined, but it is typically very near the shoulder. It never forms a "spout" nor has a siphonal canallike appearance.

The hypothesis tested was that the odd shape, a distinct "tertiary" notching of the outer lip, similar in shape to the siphonal canal, is randomly distributed throughout the species. The tertiary notch might be related to sex and/ or size (and presumably age).

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Figure 1

Aforia circinata. Scale bars = 1 cm. A. Mature male. B. Mature female; note tertiary notch on outer lip (compare with Figures 1A and 1E). C. Mature female (different from the one illustrated in Figure 1B); arrow indicates initiation of notch; note healed fractures, and how the notch is displaced after subsequent break. D. Immature male. E. Immature female; material on shell (arrow) is the remains of a hydractiniad hydrozoan; virtually all shells were covered with this material, and it had to be removed with the underlying periostracum to examine the shell. F. Mature male with a low ridge (arrow); females often had similar, albeit more pronounced ridges.





Measurements of *Aforia circinata*. L, shell length; W, shell width; Ap L, aperture length; D, distance from the shoulder carina; Wc, width of the siphonal canal; Wn, width of the tertiary notch; Hn, height of the tertiary notch.

MATERIALS AND METHODS

The specimens of Aforia circinata examined were collected from two localities in the Bering Sea, 59°20.3'N, 173°44.3'W, and 58°21.2'N, 172°19.0'W, with a 400-mesh Eastern Otter Trawl; thus, no specimens less than 50 mm long were collected. The first site, at a depth of 109 m, sampled on 25 June 1980, yielded 30 specimens; the second, at a depth of 102 m, sampled on 23 June 1980, provided seven specimens. The animals were preserved immediately in 95% ethanol. Animals from both populations were pooled for all analyses.

During examination, the snail's body was removed from the shell, the sex was determined, and an arbitrary estimate of maturity was obtained by examining the secondary sexual organs. In mature males, the penis is large, at least twice as long as the width of the mantle cavity. Males were classified as immature if the penis length was less than or equal to mantle-cavity width at the base of the penis. In mature females, the capsule gland is large and robust; generally it is three to five times the diameter of the nearby hindgut. Consequently, females were classified as immature if the capsule gland was the same diameter or smaller than the nearby hindgut.



Size-frequency distribution of the Aforia circinata examined. Length in mm.

The entire gut was dissected out, placed in a Petri dish of water, and opened to determine the contents. Two of the 37 animals examined were too badly fractured to be used for shell analysis, but their gut contents were examined.

The shell shape was noted, particularly the presence or absence of a tertiary notch. Additionally, the number of major healed fractures on the anterior three whorls was determined. On some individuals, the outer aperture lip and portions of the body whorl were badly fractured during collection; hence, the number of healed fractures could not be determined. The total shell length, the width, and the aperture length were measured. If a notch was present, its height and width were measured and its position relative to the center of the major shoulder carina was determined. The width of the siphonal canal at its narrowest point was also measured (Figure 2). All measurements were made with dial calipers to 0.1 mm.

The shell measurements were transformed into their natural logarithms for the purpose of comparing measurements, for determining differences between the snail categories of large, small, males and females, and for comparing length-to-width regressions.

The pooled samples were examined by comparing (1) the natural logarithm of the shell length to the natural logarithm of the shell width, (2) the presence or absence of the notch, and (3) the variance of the ratio of natural logarithm of shell width to the natural logarithm of shell width to the natural logarithm of shell length between and within each sex. Within-sex comparisons were based on size differences, animals less than or equal to 70.0 mm being designated "small," whereas those in excess of 70.0 mm were designated large. Examination indicated sexually mature animals always exceeded 70.0 mm in shell length.

Table 1

Shell characteristics of Aforia circinata. / = Shell fractured; thus, the number of healed fractures is undetermined.

Shell measurements (mm)			Healed fractures			
Length	Width	Aperture length	Tertiary notch	Body whorl	Mean number per whorl	
Females						
53.1	20.0	31.2	-	/	/	
54.2	20.3	31.2	-	/		
54.9	20.4	34.0	-	8	4.0	•
58.4	23.3	35.2	-	/	/	
61.9	23.5	33.6	ridge	/	/	
63.1	23.1	38.3	-	/	/	
64.6	23.9	37.4	-	6	2.6	
69.1	26.3	40.5	-	8	4.3	
71.5	26.7	36.0	-	3	2.0	
72.3	25.8	43.9	ridge	4	3.3	
72.5	28.0	42.4	ridge	/	/	
76.2	30.9	40.4	+	4	2.3	
77.5	28.0	42.4	+	/	/	
78.5	28.9	46.2	+	4	1.6	
82.3	30.1	48.7	ridge	6	2.6	
85.2	32.0	50.6	+	5	4.0	
87.7	32.4	54.6	ridge	3	2.3	
88.2	31.2	49.4	+	3	2.6	
			Mean:	$4.9~\pm~1.9$	$2.9~\pm~0.9$	(N = 11)
Males						
52.6	18.6	32.9	-	/	/	
54.7	22.5	30.6		/		
58.6	21.4	35.0	-			
59.3	22.6	27.6	-	0	1.0	
66.0	23.1	37.5	-	3	3.3	
72.3	26.0	44.1	-	4	2.0	
74.1	27.8	43.4	-	4	3.0	
75.6	27.3	43.4	-	/	/	
75.8	26.8	46.8	-	4	3.0	
80.2	26.9	45.0	-	3	1.6	
80.5	26.9	26.9	ridge	2	1.3	
81.8	31.9	50.2	-	8	4.6	
82.2	31.8	50.1	ridge	2	1.6	
84.3	30.4	49.0	-	5	2.0	
85.4	35.7	52.4	-	/	/	
85.7	32.7	51.2	-	2	1.6	
86.0	32.1	49.5	-	/	/	
			Mean:	3.4 ± 2.1	2.3 ± 1.1	(N = 11)

RESULTS

The results are unambiguous: no males have a pronounced notch, and no females smaller than 70 mm have one. All of the females that had notches were sexually mature (Table 1). Not all females have the pronounced notch, but all over 70 mm in length have either the notch or a distinct low ridge. On most of those animals with the notch, the ridge can be demonstrated at younger positions on the body whorl. Some males have a similar low ridge, albeit not as pronounced as the ridge in females. Typically, the notch arises abruptly from the ridge when the animal is about 76 mm long, and generally does not become more pronounced as the animal gets older. The notch is a hollow fold in the outer lip and is substantially smaller in all dimensions than the siphonal canal, which it superficially resembles (Table 2). Some males have a low ridge similar to the low ridge found on the smaller females, albeit not as pronounced (Figure 1).

The allometric relationship of shell width to shell shape for all *Aforia* was $\ln W = 0.98 \ln L - 0.92$. The transformed length-*versus*-width relationships were fitted by linear regressions and, with the exception of small males, no significant differences were found between the allo-

	Distance from	Tertiary notch		Siphonal canal	Shell length when notch
	shoulder carina	Width	Height	Width	first evident
	17.1	low r	idge	4.39	70.3
	16.3	low r	idge	5.82	72.3*
	18.9	1.52	3.86	4.16	74.2
	17.2	low r	idge	4.96	74.8
	19.6	3.97	2.40	5.68	76.4
	19.3	1.76	4.76	4.62	77.4
	16.1	2.64	3.46	5.47	80.0
14.0		low r	idge	5.54	80.0*
18.8		low ridge		5.82	82.0
13.8		low ridge		3.93	fractured
17.7		low ridge		5.17	fractured
	20.9	3.16	4.18	fractured	fractured
Mean	values (±1 SD)				
Ā:	17.5 ± 2.2	2.61 ± 1.01	3.73 ± 0.88	5.05 ± 0.68	76.4 ± 3.9
N:	12	5	5	11	9

Table 2

Characteristics of the tertiary notch. All measurements in mm. * = Males; all others females.

metric relationships of length to width between any of the subgroups. The large variance in the shell length-to-width ratio and the small sample size of the immature male group casts some doubt on the real significance of the difference. ANOVA on the ln width/ln length ratio revealed significant differences between large and small animals caused by the large variances within the group of small males examined.

Healed major shell fractures (determined as shell fractures after which the pattern of spiral sculpture was altered) were common in these animals, but were not significantly more numerous in one sex. The body whorl often has more healed shell fractures than either of the next two posterior whorls (Table 1); however, this is probably a function of the relative size of the body whorl. Per unit area of shell surface, no trend is apparent.

The size-frequency distribution of these pooled samples indicates no apparent differences in the male and female components. Neither sex predominates in either the large or the small size ranges (Figure 3).

No identifiable gut contents were seen in any of the specimens; in two cases, however, sand was in the hindgut.

DISCUSSION

The hypothesis that the notch is randomly distributed throughout the species is clearly disproven. The tertiary notch of *Aforia circinata* is pronounced only in mature females. Those adult females lacking a pronounced notch have a distinct ridge, lacking in most males.

The function of the tertiary notch remains unknown, although its predominance in females suggests a possible copulatory or oviposition role. MACNIEL (1960) suggested the presence of a similar notch in the deep-water turrid Pinguigemmula might be correlated with oxygen lack and thus might function as a secondary siphonal canal. In Aforia, the notch may similarly function as a subsidiary canal allowing the female to shift siphonal position to ensure an adequate flow of oxygenated water while ovipositing the tough egg capsule characteristic of turrids. POWELL (1964, 1969) dismissed MacNiel's suggestion based on the callus-filled nature of some of the notches found in the deep-water tropical turrids, a condition absent in Aforia. If the function hypothesized here is correct, the notch might be expected in species from habitats where environmental conditions would select for accessory structures to facilitate increased oxygen flow during oviposition. POWELL (1964, 1969) stated similar notches are found in a few individuals of some deep-water tropical turrids: Ptychosyrinx, Epidrella, and Gemmula hombroni (Hedley, 1922). As Aforia is also from deep water, perhaps the notches form a common solution to some problem inherent in oviposition or copulation in deep-water habitats.

Both sexes have a large number of healed shell fractures, indicating unsuccessful attempts by shell fracturing predators, presumably crabs. There was no significant difference in the number of healed shell fractures between the sexes, and the relatively even sex ratio further argues for no differential predation. *Paralithodes camtschatica* (Tilesius, 1815), *Chionecetes opilio* O. Fabricius, and *C. bairdi* Rathbun, 1893, are found nearby in large numbers. *Paralithodes*, the Alaskan King Crab, probably has the ability to attack and break the shells of *Aforia*, although it has not been demonstrated to do so.

Aforia has a long and relatively well-documented fossil record (JAVIDPOUR, 1973). Similar low ridges are seen on illustrations of several of the fossil species illustrated by JAVIDPOUR (1973): Aforia addicotti Javidpour, 1973; A. campbelli Durham, 1944; A. clallamensis (Weaver, 1916) and A. tricarinata Addicott, 1966. Indeed, one species, A. tricarinata, appears to be distinguished by the presence of just such a ridge, along with two shoulder carina. The specimens of A. addicotti and A. clallamensis figured by JAVIDPOUR (1973; figs. 12, 13) are particularly similar to A. circinata (Figure 1). It is unclear whether specimens without the ridge were collected in the same formations. If so, the sexual nature of the ridge, and subsequent notch, casts doubt upon the validity of these species in particular, and other species of Aforia described using a secondary sub-shoulder ridge as a primary characteristic.

A thorough examination of collections containing turrids from the appropriate habitats should determine how widespread the phenomenon of a tertiary notch is. If this rather peculiar shape is recognized as a normal sexual variant of shell shape and reported, then not only will data on sexual ratios of mature populations become available, but an estimate of the adaptive plasticity of the shell morphology could be obtained.

ACKNOWLEDGMENTS

I thank Mr. Paul A. Raymore, Jr., of the National Marine Fisheries Service (NOAA) for collecting the specimens of *Aforia* used in this study. The facilities of the University of Washington Friday Harbor Laboratories were used with the permission of the director, Dr. A. O. D. Willows. Earlier drafts of this paper were read by R. Fredrickson and two anonymous reviewers, who made many useful suggestions.

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